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Response diversity and resilience to extreme events in tropical dry secondary forests☆

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ABSTRACT

Response diversity, defined as the variable responses of species to environmental change, has been proposed as a key determinant of ecosystem resilience. We test this hypothesis along a tropical dry forest successional chronosequence that provides a gradient of species richness and diversity. The system experienced a strong disturbance from Jova, a category 2 hurricane, in 2011. We assessed the resilience of secondary forests to hurricane disturbance by estimating both the resistance and the rate of recovery of standing biomass, comparing data from several years prior- and post-hurricane. We assessed response diversity from variations in species-level litter production in response to fluctuations in precipitation during the annual wet-dry transition period in five pre-hurricane years. The two resilience components, resistance and recovery rate, were negatively correlated, suggesting these measures of resilience are inversely coupled. We found that historic reductions in basal area through human intervention may not necessarily reduce system resilience to additional disturbances, and may in some cases enhance the capacity to absorb hurricane perturbation. This implies old-growth forests can withstand some level of human intervention and structural change, and persist through a subsequent natural disturbance. In accordance with theory, sites with greater response diversity to climate should also be more resilient to disturbance; however, we found a surprising negative relationship between response diversity and rate of recovery. We speculate this contradictory result may be due to the compounding nature of multiple disturbances interacting with climate change, and suggest our understanding of mechanisms that confer resilience to ecosystems might need reevaluation as anthropogenic pressures related to land-use and climate intensify.

1. Introduction

Human-modified landscapes are increasingly dominated by second-growth forests, as areas cleared for human use are abandoned (Chazdon, 2008; Hansen et al., 2013). In the tropics, secondary forests are mostly growing in abandoned agricultural croplands and pastures, due to the widespread representation of this type of disturbance (Gibbs et al., 2010). Studies in the neotropics have found that, with time, regenerating forests in abandoned fields can resemble old-growth forest in various facets, including aboveground biomass (Chazdon, 2008; Poorter et al., 2016), richness (Letcher and Chazdon, 2009), and floristic composition (Norden et al., 2009), though recovery rates may widely vary depending on land-use history (Jakovac et al., 2015; Zermeño-Hernández et al., 2016), local site characteristics, distance to old-growth forest remnants, and several other biophysical factors (Álvarez-Yépiz et al., 2008; Chazdon et al., 2007). Collectively these findings suggest tropical forests possess a strong capacity to recover from this form of human disturbance, when such disturbance is not extensive, long-lasting and severe (Arroyo-Rodríguez et al., 2017; Martínez-Ramos et al., 2016).

However forest ecosystems altered by human intervention are not experiencing disturbance regimes inflicted by agricultural activities in isolation, instead they are recurrently exposed to additional disturbances, such as freezing, drought, and hurricanes, creating a confluence of multiple and overlapping pressures (Chazdon, 2003; Turner, 2010). Changes that result from human-intervention may influence how a forest system responds to subsequent disturbance (McGroddy et al., 2013; Uriarte et al., 2009), particularly as disturbances are compounded (Millar and Stephenson, 2015; Paine et al., 1998; Uriarte et al., 2009). In order to gain

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a deeper understanding on the capacity of human-altered systems to withstand multiple stressors and continue to provide ecosystem services (Millar and Stephenson, 2015; Paine et al., 1998), it is urgent to examine what mechanisms involving abiotic and biotic factors allow modified ecosystems to persist (Johnstone et al., 2016).

Tropical dry forests are experiencing multiple, interacting disturbances (Miles et al., 2006) of both natural and anthropogenic origin. In addition to widespread clearing for agriculture (Sánchez-Azofeifa and Portillo-Quintero, 2011), they experience natural disturbance in the form of tropical cyclones, with projections that suggest both storm intensity and precipitation rates may be potentially intensified in the near future (Knutson et al., 2010). Hurricanes directly impact forest dynamics related to carbon capture and carbon storage, by stripping branches of twigs and leaves, damaging or snapping stems, or uprooting entire trees (Everham and Brokaw, 1996). These changes can substantially shape forest composition and structure over a long time-frame (Boose et al., 2004). Examining two key components of forest biomass, litter production and basal area, which are sensitive to hurricane impact (Imbert and Portecop, 2008), can inform our understanding of primary production post-disturbance. Secondary tropical forests have high carbon sequestration potential (Chazdon et al., 2016) based on studies of regrowth following clearing, though seasonally dry forests may have lower capacity for recovery than other tropical forest types (Poorter et al., 2016); a deeper understanding of carbon accumulation dynamics following disturbance can clarify what role secondary forests can play in climate change mitigation strategies (Mora et al., 2017).

Central to understanding disturbance response is the concept of resilience, which describes a system's ability to tolerate an external stressor and continue functioning over time (Holling, 1973). Resilience in its broadest sense encompasses both the ability to resist change and to recover from it (Levin and Lubchenco, 2008; Mori, 2016), and thus requires the consideration of multiple components (Hodgson et al., 2015). *Resistance* is generally defined as the ability of a system to withstand or absorb the impact of a disturbance (Connell and Ghedini, 2015; Griffiths and Philippot, 2013). Recovery, on the other hand, is defined as the ability of a system to return to its pre-disturbance state; it can be measured through indicators such as *recovery rate,* the speed with which the system recovers (Grimm and Wissel, 1997; same as elasticity, per Hodgson et al., 2015). The concept of resilience has evolved to be applicable to social-ecological systems (Folke, 2016), and though there has been some disagreement on the inclusion of recovery as a facet of resilience (Connell, Nimmo, Ghedini, Mac Nally, Bennett, 2016; Sundstrom et al., 2016), it may be particularly relevant to examine recovery in order to inform active management and restoration of degraded ecosystems (Lake, 2012). Beyond characterizing the different resilience components, a deeper understanding is needed of the mechanisms that create or enhance resilience, particularly as disturbances overlap and potentially interact (Pulla et al., 2015).

The biological characteristics that confer resilience may arise through factors at the species, community, and landscape level (Oliver et al., 2015). Many theoretical studies have emphasized the importance of the 'insurance hypothesis', which suggests systems with greater diversity should maintain functioning despite environmental fluctuation (Yachi and Loreau, 1999). Specifically, this compensatory mechanism is a function of species response diversity, which measures the variability of species responses to environmental change (Elmqvist et al., 2003). A high response diversity should provide greater ecosystem resilience (Mori et al., 2012; Winfree and Kremen, 2009), because as species respond differently to the environment some may thrive while others may not, thus ensuring at least some continuity of function.

Resilience to hurricane disturbance is also influenced by stand-level structural attributes that modulate the extent of damage experienced as well as the trajectory of recovery. Trees of a greater stature (height and diameter), are more prone to damage by hurricane disturbance (Lugo, 2008; Van Bloem et al., 2005). In transformed tropical landscapes, the structural composition of a particular stand reflects both the species composition as well as land-use history (Mesquita et al., 2015). Because early successional forests are commonly characterized by a lower structural development, they may accordingly be less impacted by hurricanes (McGroddy et al., 2013). Attributes that relate to stand-level structure must be taken into account when assessing what role response diversity may play a role in predicting resilience.

Here we examine to what extent response diversity confers resilience to natural disturbance in tropical dry forests. The region of study along the Pacific coast of Mexico represents a mosaic of old-growth and secondary forest patches of differing ages. In the initial stages of regrowth following abandonment of slash-and-burn agriculture (the most common farming method), net productivity and accumulation of biomass increase over time (Anderson-Teixeira et al., 2016; Guariguata and Ostertag, 2001). With time, secondary forests in this region have been found to resemble old-growth in terms of litter production and chemistry (Bhaskar et al., 2016), forest structure (Mora et al., 2014), and functional diversity (Bhaskar et al., 2014; Mora et al., 2014). This region was directly impacted by a strong hurricane in 2011, Hurricane Jova, a category 3 hurricane (Saffir-Simpson Hurricane Wind Scale) that hit landfall as category 2, with wind speeds that reached 160 km/hour and heavy rainfall (223 mm) over a two-day period (Brennan, 2012; rainfall data from the meteorological station at Chamela). This storm allowed us to examine how human-modified forest ecosystems respond to subsequent natural disturbances. Because forest stands have different mixtures of species as a result of both spatial variation and human impact, they provide a natural experiment to test how variation in response diversity contributes to resilience of function related to biomass production.

Our objective was to empirically evaluate the conceptual framework that higher response diversity enhances resistance and rate of recovery (Fig. 1). Our specific goals were twofold: (1) to characterize the resilience of aboveground biomass in human-modified sites to hurricane impact, by estimating both recovery rate and resistance, and (2), to examine how response diversity could explain variation in resilience among forest plots. Stand-level aboveground biomass was chosen as an indicator that could assess cumulative resilience of the forest, while species' annual litter production was used to assess inter-specific variability in sensitivity to changes in water availability, as a measure of response diversity.

2. Material and methods

2.1. Study area

We conducted fieldwork within and around the Chamela-Cuixmala Biosphere Reserve, on the Pacific coast of the state of Jalisco, Mexico (19°230–19°300N, 104°560–105°040W). This tropical dry forest region experiences seasonal rainfall, and a typical annual dry season extending from November through May (Bullock, 1986). Mean annual rainfall, from 1983 to 2015, was 800.4 mm, with 87% falling between June and October (Maass et al., 2017). However inter-annual precipitation is highly variable in this region, both in terms of total and timing of rainfall (Anaya et al., 2012; García-Oliva et al., 1995; Maass et al., 2017). Areas surrounding the reserve have been largely cleared for cattle pastures and agricultural fields; some areas are subsequently left unmanaged resulting in a patchwork of secondary forests of varying age (Burgos and Maass, 2004).

2.2. Sampling

We used data from 11 sites, representing secondary forests in three categories of regrowth (young, intermediate, and advanced) as well old-growth forest with little evidence of human intervention. Secondary forests were aged 1–2 years (young), 3–5 yrs (intermediate) and 8–12 yrs (advanced) when sites were initially established in 2004. The original design had 12 sites, but the third replicate for old-growth was

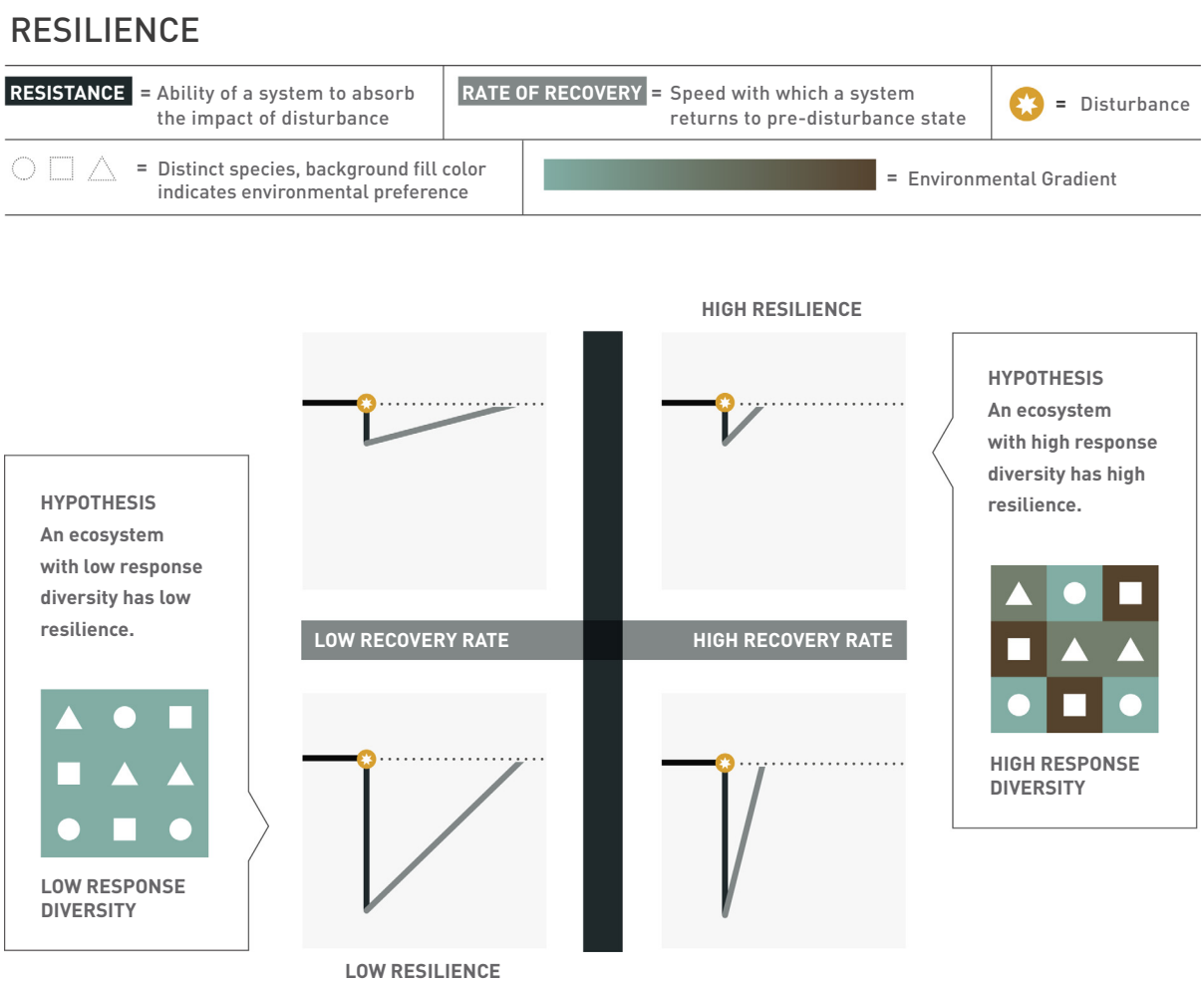

RESILIENCE
RESISTANCE = Ability of a system to absorb the impact of disturbance
RATE OF RECOVERY = Speed with which a system returns to pre-disturbance state
= Disturbance
= Distinct species, background fill color indicates environmental preference
= Environmental Gradient
HIGH RESILIENCE
HYPOTHESIS
An ecosystem with low response diversity has low resilience.
LOW RESPONSE DIVERSITY
LOW RECOVERY RATE
HIGH RECOVERY RATE
HYPOTHESIS
An ecosystem with high response diversity has high resilience.
HIGH RESPONSE DIVERSITY
LOW RESILIENCE

Fig. 1. Conceptual diagram depicting variation in two distinct components of resilience. Each of the four quadrants contains a graph of change in an ecosystem property or function (y-axis) over time (x-axis), with the gold star representing the introduction of disturbance. Quadrants on the left side versus right side depict contrasting recovery rate post-disturbance, shown through differences in the slope of the line following disturbance, with steeper slope indicative of higher recovery rate. Quadrants on the top versus bottom depict contrasting resistance (ability to absorb or withstand disturbance), shown through differences in the drop from pre- to post-disturbance levels; a shallower drop is indicative of higher resistance. Side panels detail expected role of response diversity; distinct species are represented by symbols of different shapes, and responses in the form of preferred environmental condition are shown with background fill of different colors corresponding to an environmental gradient (such as low–high nutrient inputs, rainfall, average temperature, etc.). Sites with higher response diversity, containing species with varied preferences, are expected to have higher resistance and higher recovery rate, and thus overall high resilience; in contrast sites with low response diversity (homogenous response) will have low resilience. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

dropped from this study because measurements of litterfall were sporadic and could not accurately complete several years of data. Within each site a 20 × 50 m plot was established, with plot locations designed to minimize variation in abiotic conditions, specifically soil water availability, by controlling for aspect (only south facing slopes) and elevation, ranging from 25 to 190 masl (Martínez-Ramos et al., 2012; Mora et al., 2017). Beginning in 2005 litterfall was collected monthly from twelve 0.26 m^2 circular traps in each site, and brought back to the lab to be dried, sorted by components, and weighed. Before weighing, the leaf litter component was separated from stems and other materials, and then sorted by species, for a total of 123 species. Pre-hurricane litter production data was used to calculate species response diversity (see below).

Temporal changes in basal area in each site were measured through censuses conducted every three years pre-hurricane. Within all plots, species identity, diameter, and height was recorded for all living woody stems using a size-stratified design, with diameter at breast height (DBH) greater than 1 cm for half the plot (10 m × 50 m), and greater than 2.5 cm for the other half (see Mora et al., 2017 for details). After Hurricane Jova, basal area was censused every year until 2015 when a second hurricane (Patricia) hit the region.

2.3. Species selection

In each site, a list of dominant species was determined by taking the sum for that site of all litterfall from the 5 years of data prior to Hurricane Jova, ranking by species contribution, to determine those species that contributed 80% of the total litterfall. Because most species are deciduous, and flush out at the start of June (Bullock and Solis-Magallanes, 1990), we calculated the sum of litterfall over a phenological year, defined as June through May (see Bhaskar et al., 2016 for more details). Missing data was handled in one of two ways. In four of the eleven sites, there was one month of data missing out of the entire five year span, and an estimated value was used in its place by taking the average of that particular species' litterfall for the month prior and subsequent to the missing month. In two other sites missing data was more substantial — in one of the intermediate sites (Ranchitos 3–5) six months of data were missing within the 2008–2009 phenological year, resulting in that year being dropped from the response diversity analyses for that site. However, rainfall for that year was within the range of values of other years (Table 1) therefore we do not feel it impacted our calculation of response diversity. The other instance of substantial missing data occurred in one of the three replicates of old-growth forest (Gargollo). Because sequential months of data were missing for

Table 1
Phenological year (June – May), total phenological year precipitation (mm), and extended wet-dry transition (EWDT) precipitation (October – Feb, mm). Data in bold indicate the five-year timespan during which monthly collections of litterfall were sorted by species, and then used to estimate the response diversity metric pre-hurricane.

Phenological year	Phenological year precipitation (mm)	EWDT precipitation (mm)
2005–2006	**334**	**17.0**
2006–2007	**1020**	**58.0**
2007–2008	**942.5**	**7.5**
2008–2009	**905.5**	**34.5**
2009–2010	**663.5**	**297.5**
2010–2011	835	0.0
2011–2012	1178.5	358.0*
2012–2013	837	229.5
2013–2014	1070	455.0
2014–2015	1506	470.0

* Hurricane Jova: Oct 11–13, 2011 total precipitation recorded 223 mm.

multiple years, that site was dropped entirely from all analyses, as noted above in the Sampling description.

2.4. Calculated variables

Because of the expected impact of Hurricane Jova to carbon dynamics, we were interested in calculating metrics of resilience and response diversity using measures that were informative for each and related to productivity. For estimating resistance and recovery rate we chose basal area, as a proxy for woody biomass, as this widely used measure can show cumulative impacts over time (Mora et al., 2017; van der Sande et al., 2017) and assess secondary forest resilience (Poorter et al., 2016). Changes in basal area are an indicator of carbon accumulation dynamics, and thus linked to carbon sequestration and climate regulation (Chazdon et al., 2016).

To measure response diversity, we targeted leaf litterfall as an indicator that could reveal differential species' responses to environmental fluctuation, based on the premise of the 'insurance hypothesis' (Elmqvist et al., 2003, Mori et al., 2012; Yachi and Loreau, 1999). Tropical dry forest species largely shed their leaves at some point during the dry season each year, and at the same time exhibit wide inter-specific variation in patterns of leaf phenology (Bullock and Solis-

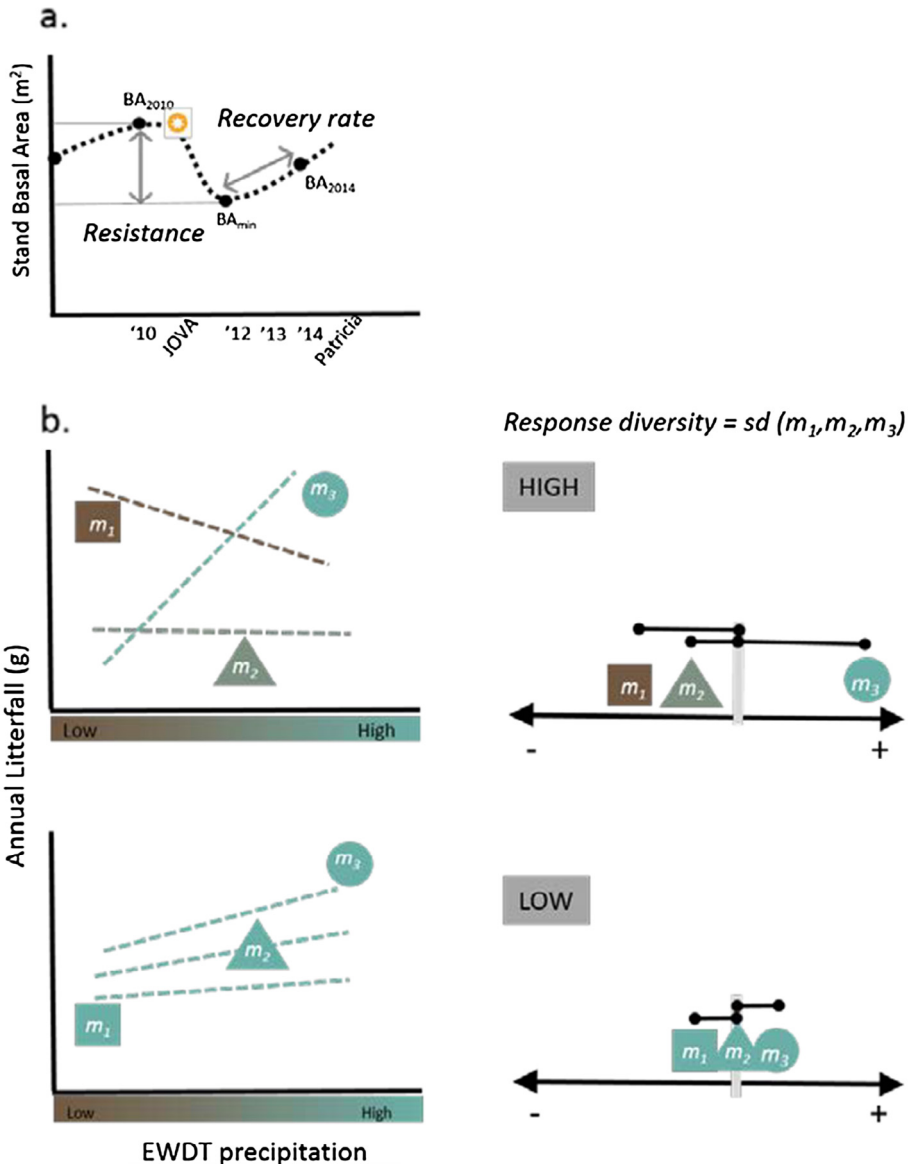


Fig. 2. Illustration of methods to calculate 2a. resilience components and 2b. response diversity. **2a**. Schematic illustrating temporal dynamics of basal area, and *Resistance* and *Recovery rate* calculations. Typical trajectory of stand basal area (y-axis) over time (x-axis). Gold star indicates disturbance, the occurrence of Jova. Black circles represent key values from census data used for calculation of resilience components. Resistance is conceptually shown as vertical arrow, and was calculated as the change in pre- and post- JOVA values: BA_{min}-BA_{2010}. Rate of recovery is conceptually shown as a diagonal arrow, and was calculated as the change in growth over time: (BA_{2014}-BA_{min})/Δt. **2b**. Response diversity. Graphs on the left depict variation in annual litterfall as a function of extended wet-dry transition period (Oct - Feb) (EWDT) precipitation for two hypothetical contrasting assemblages of three species, represented by distinct shapes (square, circle, triangle). In the top row the three species have distinct responses to precipitation, with annual litterfall either decreasing (m1; square brown fill), increasing (m2; circle blue fill) or unchanging (m3; triangle grey fill) in years of higher rainfall. In the bottom assemblage all species have positive increases in annual litterfall with increasing EWDT precipitation (square, circle, triangle with blue fill). The slope estimates of the three co-occurring species are plotted on a number line and shown in relation to the mean, depicted with the grey vertical bar, which is the same in both top and bottom assemblages. The deviation of each point to the mean is depicted with black horizontal lines, to illustrate high standard deviation (top) or low (bottom), corresponding to high or low response diversity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Magallanes, 1990; Martínez-Yrízar and Sarukhán, 1990). Multi-year studies of litterfall document the importance of water availability, as a driver for changes in litter production for many species (Bullock and Solis-Magallanes, 1990, Martinez-Yrizar et al., 2017). Litter is widely recognized as a good indicator of net primary productivity in tropical forests (Aryal et al., 2015; Malhi et al., 2011), including in this particular seasonally dry forest system (Martinez-Yrizar et al., 1996). Therefore we felt litter production was a suitable choice for estimating response diversity, in that it is variable among species, sensitive to environmental change, and informative to understanding changes in productivity.

We expected variation in leaf litter production would be a good predictor of resilience in basal area because higher annual litter production indicates a greater investment to photosynthetic tissue, and therefore net primary productivity, which in turn should result in a greater incremental change in woody biomass (Malhi et al., 2011). Consistent with this expectation a positive linear relationship has been observed between canopy production and woody allocation in many Neotropical forests (Malhi et al., 2011), including among our plots (Supplementary Fig. 1). We further validated our expectation by examining whether changes in basal area pre-hurricane were associated with changes in litter-production. We first used a linear model to test for a positive relationship between changes in litterfall and basal area based on pre-hurricane data collection, across all species from our plots. Subsequently we did a second analysis to include the effect of interspecific differences, including only a subset of species that had data from at least two different sites, resulting in a subset of 20 species from our 60 species total. For both tests, the relative changes in basal area were estimated for each species in each site, using the ratio of the difference between the 2010 and 2007 censuses relative to the 2007 basal area, and similarly relative changes in litter production were estimated using the difference between the 2009–2010 phenological year and the 2006–2007 phenological year, relative to the 2006–7 phenological year annual production.

Using the measures of basal area as an estimate of aboveground biomass, we calculated two different components of resilience: resistance and recovery rate (Fig. 2a).

Resistance was calculated as

$$\text{Resistance} = BA_{min} - BA_{2010}$$

where BA was the sum of the basal area for each site, for all stems in the census. The 2010 value was from the census pre-hurricane, and the minimum post-Jova value, BA_{min}, from whichever year that particular site had the lowest basal area value. For almost all sites this was 2012, though for one site it was 2013. We used the minimum post-hurricane basal area value to capture the full change in state resulting from disturbance (Hodgson et al., 2015). A more negative value indicated a greater drop from the pre-hurricane value, and therefore lower resistance.

Recovery, in a resilience context, is generally defined as a return to a prior or pre-disturbance state (Hodgson et al., 2015) or to some form of equilibrium (Connell and Ghedini, 2015); however, empirically measuring a rate of recovery is complicated because it may not follow a linear trajectory and in fact rates have been found to change over time following disturbance (de la Riva et al., 2017). In addition, our study was unable to encompass a sufficient period to determine if and how the pre-disturbance state was reached, due to the arrival of a second hurricane, Hurricane Patricia, in October 2015 (Kimberlain et al., 2016). Therefore we chose to focus on the *initial* rate of recovery, and we used the 2012–2014 period as the best estimate of how the trajectory was proceeding immediately following Hurricane Jova, and prior to Patricia.

Initial recovery rate was calculated as

$$\text{Recovery rate} = (BA_{2014} - BA_{min})/\Delta\text{time}$$

Response diversity is defined as the variability in responses among organisms to environmental change (Elmqvist et al., 2003; Karp et al., 2011). We used a five-year dataset of litter production, prior to the impact of Jova, to assess differential species responses, in terms of litter output, to precipitation. While total annual precipitation can influence annual litter production in tropical dry forest systems, there is substantial variability at the regional scale (Lawrence, 2005), potentially reflecting changes in species composition. The high year-to-year variability in the region of study suggests that in addition to interspecific differences, litterfall is influenced by different environmental variables (Martínez-Yrízar and Sarukhán, 1990). Analyses of various climatic measures have found that the amount of rainfall during the transition from wet to dry season, between November-February, is a good predictor of total litter produced annually, as this is the period when most species drop their leaves (Bullock and Solis-Magallanes, 1990; Martínez-Yrízar and Sarukhán, 1990). This may be because rainfall during these typically dry months serves to extend the window for some species to continue leaf and thus litter production (A. Martínez-Yrízar, unpublished). Accordingly, the annual litter production has been observed to be above average in years with higher than normal rainfall during this transition period (Martinez-Yrizar et al., 2017). Meta-analyses of water-limited tropical forests have generally found that carbon assimilation, and therefore litter production, is sensitive to seasonal variation in precipitation (Wagner et al., 2016). Rainfall during the transition period may have the effect of reducing the duration or intensity of the dry season, which in turn has been found to directly impact forest productivity (Murray-Tortarolo et al., 2016). The timing of Jova, which hit in mid-October, highlights the importance of including species' sensitivity to rainfall during this month as well. Therefore our measure of response diversity focused on interspecific responses to precipitation falling during what we call the "extended" wet-dry transition period (EWDT), defined here as October through February.

To calculate our response diversity metric, we first fit a linear model for each site, with species, EWDT precipitation, and their interaction as explanatory variables and annual litterfall as the response variable. Other studies have used a similar statistical approach, and have inferred from a significant interaction term that response diversity is detected in a particular system (Karp et al., 2011; Winfree and Kremen, 2009). However, we were interested in not just the presence but the degree of response diversity, in order to compare across sites. We calculated our novel metric of response diversity by focusing on the variation in slope of the precipitation-litterfall relationship among species, using the *coefficients()* function in R to extract the model estimates of the slope for each species. Our observed site-level measure of response diversity was calculated as the standard deviation of these slope estimates which provided an aggregate measure of the variability of species' responses within a given site (Fig. 2b).

Previous work has shown that the number of species that contribute to the bulk of stand-level biomass (defined at 80%) varies among plots and, in particular, changes systematically among secondary stages with increasing recovery time (Bhaskar et al., 2014). Since response diversity could increase as a function of species richness, we controlled for the potential confounding effect of species richness by using a null model approach (see Supplementary Fig. 2). The null model approach consisted of simulating different combinations of species assemblages through random sampling of our complete data set. We compiled our entire pool of observations, keeping species found in multiple sites as distinct samples, such that we had a total of 123 measures of litterfall response to precipitation. From this pool we generated random assemblages that covered a range of species richness (from 3 to 20) that spanned the numbers of species found in our 11 sites. At each richness level 1000 different random assemblages were sampled, by drawing with equal probability from our pool of 123 total observations, and the slope standard deviation was calculated for each assemblage. The average of the 1000 draws was calculated for each richness level, as our estimate of expectation/tendency of this metric. The response diversity

divergence was the difference between the observed site-level measure and the expected standard deviation derived from the null model for the same level of species richness.

2.5. Statistical analyses

Our central hypothesis concerned the role of response diversity as the mechanism that might explain variation in resilience-components. To take into account the expected influence of stand structure, we included stand development as a covariable in our analyses. We used a linear model, the *lm()* function in R (version 3.3.0, R Development Core Team 2016) to test whether resistance to hurricane damage was influenced by the response diversity of the constituent species. Because the size of the stand prior to disturbance could influence resistance, we included the basal area measure from 2010 as a co-variate for statistical control. Similarly, we tested whether variation in recovery rate was explained by site-level response diversity. In the recovery rate model we included the lowest stand basal area post-hurricane as a co-variate, to control for any influence of stand size on growth-rate during the recovery period. Variables were log-transformed as needed to meet the assumptions of normality and variance homogeneity. We used the *Anova()* function in the *car* library to calculate a Type II sums of squares, to assess the significance of each factor.

Because of the small sample-size, we also conducted a Cook's distance analysis to identify any influential data points and ensure that our results were not driven by a single outlier.

3. Results

Comparing changes in basal area with those in litter production from pre-hurricane years, we found a significant association across all species (Supplementary Table 2). A positive coefficient estimate (0.2) indicated that increases in relative litter production were associated with increases in relative basal area, but there was overall low explanatory power of the model. We found that including the Species term in our second test, using a subset of species, improved our model (R^2 = 0.87 vs 0.26; Supplementary Table 2), and again indicated that relative changes in litterfall were significantly associated with relative basal area growth, though the strength of the relationship was species-dependent.

The five-year timeframe in which we measured litter production before the onset of the hurricane happened to span a period when annual precipitation varied by 2.5-fold (Table 1). The years from 2005 - 2010 included one of the driest years on record (Maass et al., 2017) when in 2005 total annual precipitation was under 400 mm, as well as above-average wet years with precipitation near 1000 mm. Rainfall during the extended wet-dry transition (EWDT) period also varied among years in this 5-year window, and ranged from less than 10 mm to over 400 mm (Table 1). Thus, our pre-disturbance study period captures substantial inter-annual climatic variability, similar to the long-term 1985–2009 range (Maass et al., 2017), which in turn should provide sufficient range to detect differential species responses.

In comparison to the pre-hurricane years of the last three decades, the region received a high input of rainfall from October 11–13th, 2011, due to Hurricane Jova. This storm resulted in a precipitation input over a short time duration that was substantially higher than the total received over the EWDT period of most previous years. Subsequent to Jova, the three years that followed also had consistently greater than normal quantities of rainfall in this period (Table 1).

A wide range in resilience values was observed among sites, both for resistance and recovery rate, in response to Hurricane Jova (Table 2). Most of the sites (7 out of 11) experienced a decrease in the total stand basal area following the hurricane compared to pre-hurricane values, as indicated by the negative values calculated for resistance. However some sites did have positive resistance values, which could be a result of either no loss in basal area or a loss and subsequent rapid recovery. Due to the timing of census collection, we cannot distinguish between these two possibilities, as only net basal area change between 2010 and 2012 is available, thus any losses or gains in basal area that occurred in between cannot be discerned. Because the damage to trees is used in the calculation of response variables we did not have any independent measure of hurricane impact, thus we had to assume all sites were in the trajectory of the hurricane and experienced a similar level of impact. In the four years following Hurricane Jova and before Patricia, all sites experienced positive incremental growth in stand basal area, as indicated by non-zero values of recovery rate. These rates of recovery varied nearly 40-fold between the lowest (117 $cm^2\ yr^{-1}$) and highest ($\sim$4570 $cm^2\ yr^{-1}$) values.

Sites with the highest resistance to Hurricane Jova did not necessarily have the highest rates of recovery, in fact resistance and recovery rate were significantly negatively associated (Pearson's correlation = -0.83). This suggests that the two dimensions of resilience (i.e., resistance and recovery rate) are inversely coupled. Rather than exhibiting high resistance and high recovery rate, as shown in Fig. 1, resilience is achieved by occupying one of the quadrants along the top-left to bottom-right diagonal. In other words, sites were observed to exhibit resilience by being resistant or recovering quickly, but not both.

Inter-specific differences in sensitivity to rainfall variation during the EWDT period were found from analysis of annual litterfall patterns of individual species over the five years prior to Jova. As shown in Supplementary Fig. 3, annual litterfall for individual species plotted against EWDT precipitation illustrates that slopes varied in both direction and magnitude. On average slopes were positive (data not shown), suggesting most species increased litterfall in years with higher EWDT precipitation. Overall, our model, which included as predictor variables a species term to account for differences among species, variation in the amount of EWDT rainfall, and species by rainfall interaction, explained a substantial portion of the inter-annual variation in litterfall, as indicated by the high adjusted R^2 values (Supplementary Table 1). Our estimate of response diversity, a measure of the collective standard deviation among slopes of co-occurring species (Fig. 2b), was not sensitive to species number, with little variation when compared to the null model (Supplementary Fig. 2). The observed response diversity of our 11 sites did not increase in sites with a greater number of species; in fact, if anything, sites of higher species richness tended to have values lower than expected based on the null, while those with lower species richness fell above the null expectation line. We found no qualitative difference in the statistical models when we used observed response diversity versus divergence from the null model, so we report only the former. The variation we observed among sites (ranging from 0.04 to 0.32; Table 2), was in part due to differences in species composition (data not shown). Sites with high response diversity were those that included dominant species with diverging slopes, leading to a higher standard deviation (see Fig. 2b).

In contrast with our expectations, we found that response diversity did not explain variation in resistance to Hurricane Jova (Table 3). While we expected a positive relationship between sites with high response diversity and those with high resistance, no association was found. Resistance did, however, seem associated with the stand size prior to hurricane impact; sites with a higher basal area in 2010 experienced a larger decrease in basal area post-Jova, and thus exhibited lower resistance (negative coefficient in Table 3; Fig. 3a).

Recovery rate, in turn, was significantly associated with variation in response diversity, but surprisingly the relationship was negative (Table 3). In direct contrast to our hypothesis, sites with higher response diversity were those with a lower rate of recovery (Fig. 3b). We had in addition expected that sites with a lower basal area following Jova might be those that experienced a higher growth rate and thus higher recovery rate, however we found no significant relationship between it and minimum basal area (Table 3). We found the significant negative effect of response diversity remained even after exclusion of one site (Zapata), which seemed to be an influential point based on

Table 2
List of sites names and measured characteristics. Successional age category, replicate number and site name (in parentheses), basal area pre-Hurricane Jova (2010), resistance, recovery rate, species richness (number of dominant species included in that site), and response diversity, as measured by standard deviation of slope estimates of species responses to EWDT rainfall.

Successional stage (Site name)	Basal Area Pre-Hurricane Jova (2010) (m^2)	Resistance (m^2)	Recovery rate ($m^2\ yr^{-1}$)	Dominant species richness	Response diversity
Early 1 (Pastizal San Mateo)	5325.8	1098	758	7	0.12
Early 2 (Pastizal Santa Cruz)	2649.5	−101	950	8	0.15
Early 3 (Pastizal Zapata)	2139.3	154	117	3	0.32
Intermediate 1 (3–5 Caiman)	7876.9	255	2218	12	0.07
Intermediate 2 (3–5 Ranchitos)	6482.9	2606	1814	9	0.08
Intermediate 3 (3–5 Santa Cruz)	7482.9	−2097	2611	5	0.07
Advanced 1 (8–12 Caiman)	17812.1	−2450	2105	15	0.07
Advanced 2 (8–12 Ranchitos)	12572.7	−1267	1247	8	0.13
Advanced 3 (8–12 Santa Cruz)	16813.3	−5302	3468	12	0.04
Old Growth 1 (Tejon 1)	18428.1	−680	1143	10	0.11
Old Growth 2 (Tejon 2)	24186.1	−10381	4570	13	0.09

Table 3
Effects of response diversity and basal area on resilience components (Resistance and Recovery Rate).

	Resistance			Recovery rate (log)		
	F	*p*	Coefficient	*F*	*p*	Coefficient
Basal $area_{2010}$	11.4	**0.009**	−0.41			
Basal $area_{min\ post\text{-}Jova}$ (log)				0.08	0.8	0.07
Response diversity	0.33	0.58	−6.9e+3	28.4	< **0.001**	−11.8

Cook's distance measure.

4. Discussion

Ecosystems increasingly face multiple anthropogenic stressors that interact in complex ways (Didham et al., 2007; Foster et al., 2016) to impact system resilience (Folke et al., 2004). Thus it is urgent to develop management strategies to actively promote resilience of secondary forests in light of climatic change and other human-induced disturbances (Millar et al., 2007), but this requires a deeper understanding of how disturbances interact (Foster et al., 2016), as well as the mechanisms that allow modified ecosystems to persist.

We adopted the theoretical framework that resilience can be decomposed into resistance, the extent to which an external disturbance is absorbed by a system, and recovery rate, reflecting the capacity to return to pre-disturbance conditions (Fig. 1). The theoretical separation into these two components was consistent with our results that showed that these measures may vary inversely. Our findings highlight that future studies should continue to consider these as distinct components that collectively describe resilience. Separating the two components provides the opportunities to identify strategies or mechanisms that may be driving one facet of resilience but not necessarily the other (de la Riva et al., 2017; Van Ruijven and Berendse, 2010), as we observed here. This work offers support to the argument that recovery should be explicitly incorporated within a resilience framework (Mori, 2016), as it provides a more complete understanding of mechanisms that can inform management and planning (Nimmo et al., 2015).

Resilience of tropical secondary forests stands, those that have experienced historical disturbance in the form of slash-and-burn clearing, was comparable to those of old-growth forest. Several of the secondary forest plots showed no evidence of a drop in stand-level basal area post-Jova, suggesting a high capacity to absorb additional disturbance in the form of high resistance. The lower basal area of these previously disturbed stands may in fact impart such resistance, consistent with previous results that stands of smaller basal area, which tend to be secondary forests, undergo less structural damage (McGroddy et al., 2013). Therefore, management of forests may not necessarily result in lower resistance, in fact there may be some resistance to hurricane disturbance that could increase as a result of human intervention, as in this case via agricultural management.

Exposure to previous disturbance, including forest management and forest conversion into agricultural land followed by abandonment, may promote resilience to subsequent disturbance through structural and biomass-level changes. This has been shown in fire-prone systems, where forest management reduced fuel-load and enhanced resilience to larger disturbances (Davies et al., 2009). However changes in composition need to be factored in when assessing the implications of structural changes. In this study, species composition in most of the secondary forests resembles that of old-growth (Bhaskar et al., 2014). However, in other systems, where disturbance is accompanied by composition shifts, secondary species have proven less resilient to disturbance than the old-growth forest species (Foster et al., 1998). Further, there may be differences in resistance to damage from hurricane even among secondary forest species, and in fact at the species level smaller basal area individuals may be more vulnerable to damage (Ostertag et al., 2005). Therefore though reductions in stand-level basal

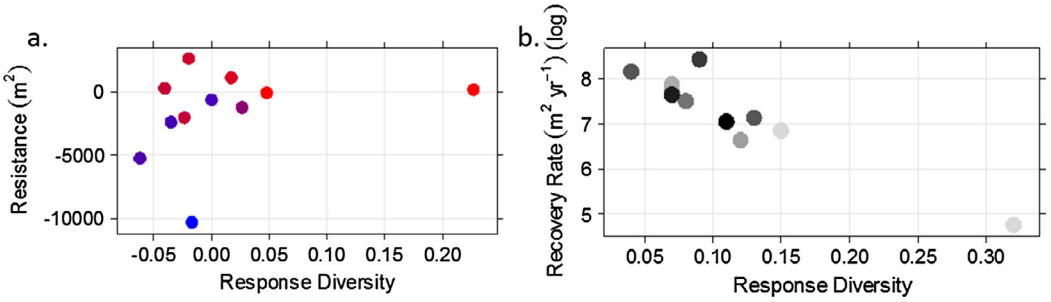
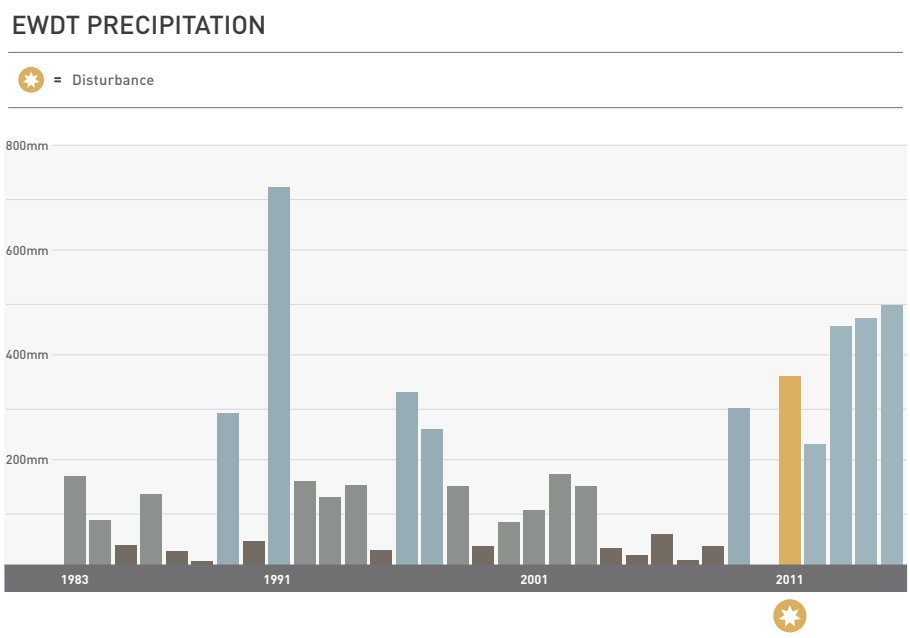


Fig. 3. Resistance (3a) and Recovery rate (log) (3b) versus Response Diversity. Data points represent each site, color-coded by site-averaged basal area in 2010 pre-hurricane (gradient of low (red) to high (blue) basal area) in 3a, or minimum basal area post-hurricane (grey scale, larger basal area in darker grey) in 3b. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



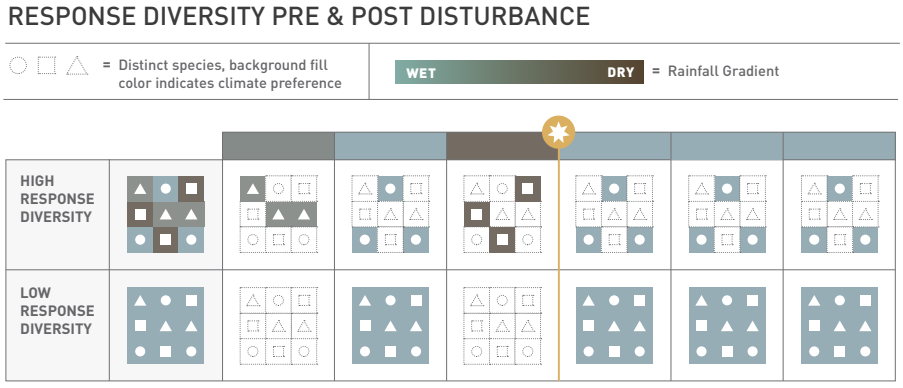


Fig. 4. Species responses to pre- and post- disturbance climate variability and impacts on system level function for sites with contrasting high and low response diversity. 4a. Recorded precipitation data (mm) for extended wet-dry transition period (EWDT) color-by rainfall gradient. Gold star indicates period of Hurricane Jova. 4b. Conceptual representation of pre- and post-disturbance response of sites with matching species richness (three species, shown with distinct shapes) and high (top row) versus low (bottom row) response diversity. Colored bars indicate different years. Species precipitation preferences and year bars are color-coded to indicate EWDT precipitation level. In years matching climate preference species are displayed with colored background fill to indicate max performance, versus years of non-preferred climate, when species are outlined to indicate little to no contribution to ecosystem functioning. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

area from human intervention may impart greater resistance, it may also include important species-level changes that need further study.

In accordance with the insurance hypothesis, we expected that stands with higher response diversity would have higher resistance and recovery, however unexpectedly we found the opposite. Theory predicts that assemblages of species with diverging responses provide greater ability to maintain function at the ecosystem scale in the face of environmental perturbations — while some species may suffer others may benefit (see (Yachi and Loreau, 1999). Yet we found that sites with higher standard deviations in their slope estimates tended to accumulate carbon more slowly in their recovery phase, compared to those sites with more homogenous slopes. Because of the small sample-size of this work, and the few existing studies assessing the role of response diversity (Mori et al., 2012), more empirical studies are needed to evaluate the generalities of this finding. We propose a few directions below that future studies might address, related to the choice of metric and indicators, which can add to our understanding of the role of response diversity as a mechanism conferring resilience.

We employed a novel metric to calculate response diversity that is largely consistent with other empirical work, in that it employs a linear model (see for example Karp et al., 2011; Winfree and Kremen, 2009). This approach presupposes that species responses are linearly proportional to some environmental variable; however, not all species litterfall responses may be accurately represented with a linear fit (Supplementary Fig. 1). Another approach that could be valuable to develop could draw from work quantifying species phenology along a gradient of synchronous to compensatory dynamics (Lasky et al., 2016), to incorporate non-linear responses when calculating response diversity.

We chose to use two distinct indicators to assess response diversity and resilience, using reasoning similar to that behind categorizing functional traits into a response-and-effect framework (Suding et al., 2008). Namely, for response diversity we wanted a measure that would be able to indicate differential species responses to the environment, similar to response traits, and separately for resilience we sought a measure that would allow us to scale-up, to quantify the effect, or contribution, to a longer-term ecosystem function (Mori et al., 2012). Other variables are also worth considering for the calculation of one or possibly both metrics, and we would highlight resprouting capacity as a species trait that shows differential post-disturbance response and could prove important in understanding carbon accumulation dynamics, particularly in tropical dry forest systems (Lévesque et al., 2011, Mora et al., 2017).

We expected the two chosen indicators to be associated, and observed that changes in litterfall could be informative to predict changes in basal area (Supplementary Table 2). However these associations were observed pre-hurricane Jova. Species responses following disturbance have been found to change in rate and direction over time (de la Riva et al., 2017). In addition to interspecific variation, different carbon pools may have different rates of recovery (Guariguata and

Ostertag, 2001) and follow non-linear trajectories following hurricane disturbance (Imbert and Portecop, 2008). Further, even when different carbon components including wood productivity and litterfall have been found to be responsive to the same climatic driver in water-limited environments, there may be a time lag that results in responses not being synchronized (Wagner et al., 2016). Collectively, these studies suggest complex dynamics that occur over longer time scales than we were able to monitor, because of the arrival of a second hurricane. Therefore the post-disturbance period of study may not have been of sufficient length to detect a longer-term association. Future studies may be able to add to our understanding of whether response diversity has differential predictive ability for initial versus later recovery or through the use of indicators that integrate over different timescales.

One additional factor that warrants exploration is the poor accord between environmental conditions prior to and subsequent to the impact of Jova. Rainfall during the EWDT for the 5-year pre-event timeframe when response diversity was calculated spanned a range that encompassed what has historically been observed in the region (Maass et al., 2017); post-disturbance, however, the mean value was shifted, as repeated years had well-above average rainfall (Fig. 4 panel a). In fact the 2011–2015 period encompasses sequential years of high rainfall during the EWDT unlike what has been seen in the region in the 20 years prior to Jova (Fig. 4). One reason for this is that a second hurricane (Patricia) hit in 2015 (Kimberlain et al., 2016) which caused a much larger canopy and tree forest impact (Parker et al., 2017; Martínez Ruiz and Renton, 2017). The frequency and magnitude of such hydro-meteorological events has historically been much lower; thus the occurrence of two intense hurricanes only 4 years apart might represent a shift towards increasing storm frequency, consistent with model forecasts for this zone of the world (Knutson et al., 2015).

We speculate that the shift in climatic conditions pre- and post-disturbance might be contributing to the relationship between response diversity and recovery. During the pre-disturbance measurement period, the collective average slope for all the species in our study was positive, in other words species tended to have higher annual litterfall in years with higher EWDT rainfall. However, sites with high response diversity, by our definition, were those with heterogeneous slopes, thereby including species with low or no preference to high precipitation (Fig. 2b, Fig. 4). Extrapolating these responses post-disturbance, this would suggest that those sites with a homogenous response (and thus lower response diversity) would contain species largely receptive to the elevated precipitation found post-disturbance (Fig. 4a), resulting in greater performance by those species due to multiple years of favorable climate (Fig. 4b). Consistent with this hypothesis, a parallel study of annual site-level litterfall in old-growth forest sites within the same dry forest system has found higher than average litterfall rates in the two years when hurricanes struck (Hurricane Jova and Patricia), as well as in the intermediate years when rainfall during the dry season continued to be elevated (Martinez-Yrizar et al., 2017). Though some species will experience greater productivity as a result of elevated rainfall, the range of response diversity indicates other species will not benefit, lending support to the idea that seasonally dry tropical forests will be vulnerable to changes in rainfall regimes (Allen et al. 2017).

The unexpected relationship between recovery and response diversity may highlight a need to re-consider resilience mechanisms (Folke et al., 2004), by explicitly considering the influence of pre- versus post- disturbance climate (Johnstone et al., 2016). The mechanism of response diversity is framed around disturbance as a discrete event; however, changes to the climatic background prior to and subsequent to the discrete disturbance event may complicate the role of response diversity (Fig. 4). This study adds to an emerging body of work that suggests species responses formed under 'typical' historical conditions may have a reduced capacity to contribute to post-disturbance recovery when climate follows an atypical pattern (Harvey et al., 2016; Johnstone et al., 2016; Rother et al., 2015). In fact, differential responses to post-disturbance climate can lead to shifts in species and functional composition compared to that pre-disturbance. This is seen in a subalpine forest system, where recruitment post-wildfire was significantly influenced by the type of climate that persisted in the period post-disturbance; species that were dominant pre-fire were particularly prone to low recruitment as a function of drought severity, suggesting the post-disturbance climate could shape community composition and thus the recovery trajectory (Harvey et al. 2016). Our contribution may be an example of interaction modification, depending on whether the level of one stressor (atypical rainfall variability) modifies the effect of the other (hurricane disturbance) (Foster et al., 2016), but this needs further study.

The implications of climate (i.e., rainfall variability) on recovery are a form in which disturbance can have a long-term legacy impacting resilience (Johnstone et al., 2016). Though systems may experience recovery, the duration of recovery may be incomplete. A recent analysis reveals that systems experiencing disturbance may suffer a loss of system functioning that persists well after disturbance event is over; quantifying this recovery 'debt' as it accrues over time illustrates the widespread impacts to diversity and abundance (Moreno-Mateos et al., 2017). As climate disturbance frequencies increase, even those sites with high recovery rates may not experience a sufficient interval to restore to pre-disturbance conditions (Moreno-Mateos et al. 2017), particularly if climate change creates a novel post-disturbance environment.

5. Conclusion

Overall we find evidence that the interaction between different disturbance types (natural and anthropogenic) creates varied outcomes for forest ecosystem resilience. Prior historical human management can confer resistance to subsequent infrequent disturbance, but recovery from disturbance in the context of varying climate is complex. The potential interaction between disturbance types has not been explicitly incorporated in a resilience framework, which typically considers the influence of a single perturbation event. Due to the rate and reach of climate change, systems such as tropical dry forests experience almost a constant background disturbance on which these other disturbances are overlaid.

Our findings showed that forest management that decreased basal area, in this case via transformation into agricultural land and subsequent abandonment, increased, rather than decreased, forest resilience. This suggests that intentionally manipulating forest basal area could be used to promote forest resistance, although long-term study post-disturbance would be needed to evaluate any resulting shifts in forest composition. Our findings also suggested that response diversity was negatively correlated with resilience, in part we speculate because the post-disturbance climate differed markedly from the long-term trend, and happened to favor the responses in low-diversity sites. We propose that further studies are needed to examine the role of different types of indicators, as well as multiple overlapping perturbations in the context of a changing climate, in order to develop strategies to actively promote resilience of tropical dry secondary forests.

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Appendix A. Supplementary materail

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2017.09.028.

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